NOTES ON THE LIFE HISTORY OF *AMBYSTOMA TIGRINUM NEBULOSUM* HALLOWELL IN UTAH

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The early life history of *Ambystoma tigrinum*, as it occurs in Utah and adjoining areas, has long been in need of study. A few studies have been conducted. Dr. V. M. Tanner (1931) provided us with the most important natural history information to date for this salamander. However, he was concerned primarily with its distribution in Utah and its food habits. Skousen (1952) studied the egg and early larval development of only a few eggs but did provide some pertinent information concerning the size of eggs and hatchling larvae. Hamilton (1948) reported the egg-laying habits of this subspecies from Muskee Lake, Colorado. Webb and Roueche (1971) have provided a rather complete life history study for a population of *Ambystoma t. mavortium* at Taylor Well, approximately 19 miles northeast of Las Cruces, New Mexico.

This study is confined to observations of the eggs, developing larvae, their growth rate, and the dates of their appearance as active larvae. A study of the food habits by means of stomach analysis from larvae and adults and an examination of early embryology will be reported at a later date.

Salamander Lake in Stewart Canyon on the northeast slope of Mt. Timpanogos (Utah) was selected as the study area (Figs. 1 and 2). The ease of access and the fact that it is fed and drained by the ground table water rather than flowing streams made this lake an ideal habitat for a study of larval salamanders.

Data have been gathered by four individuals. Unfortunately, each has been unable to complete the study for lack of time or other reasons. However, all the data available were obtained from Salamander Lake and involve the same breeding population. The data gathered by Skousen were taken in 1950; by Fisher in 1967; and by Willis in 1970-71.

Fisher did not find eggs and his data are primarily concerned with developing larvae and ecological conditions effecting growth.

Willis found the eggs and observed a female as she laid eggs in a large aquarium. Hatching was observed, and the early stages of larval development were studied. With the data from Willis, the life cycle can be generally outlined.

Eggs and Egg Deposition

The first eggs were secured by Skousen on 26 May. Only two

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Fig. 1. Salamander Lake 8 June 1967, showing the lake at near capacity.

Fig. 2. Salamander Lake 20 August 1967, same view as figure 1 showing the abundant growth of plants in the reduced water.

eggs were measured, and these had the following dimensions (unpublished M.S. thesis):

Outer Casting	Envelope I	Envelope II	Envelope III	Vitellus
9.1	5.1	4.6	3.9	2.2
8.5	5.4	4.6	3.8	2.1

Willis first visited the lake on 3 May 1971. There was snow in rather large patches near the lake, and it appeared as though the ice had only recently melted. A number of large larvae were present in the lake. Five larvae ranged in size from 77 to 111 mm, total length, and 42 to 60 mm in S-V length. Four adults were seen on 13 May, and, of these, 3 were males and 1 a female. On 15 May, the weather was misty and a light rain continued during the day and into the evening. Apparently the rain stimulated emergence; at least by the next day, 25 adults were counted in the lake.

Eggs have been seen and/or collected by us and other students at Salamander Lake and other nearby locations, however, the observations made by Willis concerning the eggs and oviposition are the most complete. A gravid female (98 mm S-V) taken on 15 May and placed in an aquarium laid a clutch of eggs on 16 May. The size of the vitellus in 11 of these laid on a small twig had a range in diameter of 1.7-2.5 and averaged 2.12 mm. The average compares well to that of Skousen and to that reported by Webb and Roueche (1971). We found it difficult to measure accurately the dimension of the surrounding envelopes owing to the position of the attached eggs. We did confirm, however, that there was considerably more variation in the diameter of the various envelopes than we noted in the vitellus.

The eggs were laid singly or deposited in pairs or in strings ranging in numbers from 3-4 to as many as 15 in one linear string. Eggs are laid on either floating or submerged twigs, rocks, or on the stems of growing vegetation. In all instances, the eggs were attached to an object. We saw none that were floating free or were loose on the bottom of the lake or the aquarium. We note that there were no egg clusters. Each egg, as it is laid, is attached by the outer gelatinous layer to the object on which it is laid. The observations of Willis indicate that each egg is laid separately, that is the female possesses the ability to produce one egg at a time and to place it on the object selected for its deposition. The fact that more than one egg was laid, and that they may occur in rows, seems to be coincidental to the fact that egg laying, and where each egg is deposited, is controlled by the female. This allows her to distribute the clutch in many areas throughout the lake.

The eggs hatched on 22 May, beginning at approximately 3:00 PM and continued until 8:00 PM, 155 hours from the time they were laid. The water in the aquarium was maintained at approximately 19 C (room temperature). Skousen reports 2-3 weeks from the time eggs were laid in the lake until hatching, and Webb reports

204 hours (8.5 days) in the laboratory at 25 C for the New Mexico population.

A series of 24 hatchlings (May 1971) were preserved and measured soon after they had been freed from the gelatinous egg mass. They ranged in size from 9.1 to 13.6 mm and averaged 11.9 mm. At this early stage, the larvae are distinctly tadpolelike, having a large head, three pair of external gills, well-developed black eyes, but without legs and with little pigmentation. The front legs appear in larvae 17 to 20 mm in total length. Hind legs were not seen in larvae less than 25 mm long.

Larval Growth

During the summer of 1967 (June through August), Lowell Fisher studied the larvae at the lake. Larvae were obtained from the lake by means of a large aquatic insect net with a one-foot-square opening and all specimens were preserved immediately in 10 percent formaldehyde.

The total length of all larvae were taken in millimeters and placed on a graph for comparison. Temperatures of water and air were recorded. The precipitation data were supplied by Mr. E. Arlo Richardson—the weather bureau climatologist of the Department of Soils and Meteorology at Utah State University, Logan (Fig. 3).

The first larvae of the summer were taken on 2 July. Weekly collections were then made until the end of August. The sudden appearance of small new larvae on 30 July presented an interesting but perplexing problem. Comparisons between the newly hatched larvae and rainfall data indicated a distinct correlation between precipitation and breeding times (Fig. 4). The egg-laying to hatching time of two weeks as reported by Skousen (1952), and the rainfall data from Richardson, seemingly provide the solution (Fig. 5). It was also noted that the only appearance of adults during the sum-

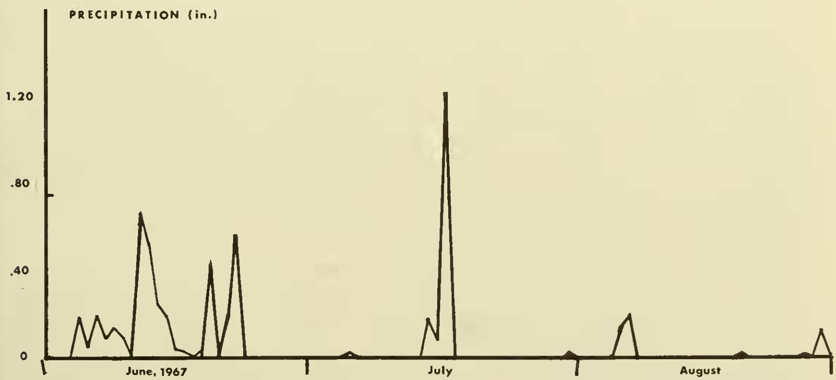

Fig. 3. Precipitation from 1 June 1967 to 31 August 1967, taken from the records of the National Forest Weather Station a short distance from the lake.

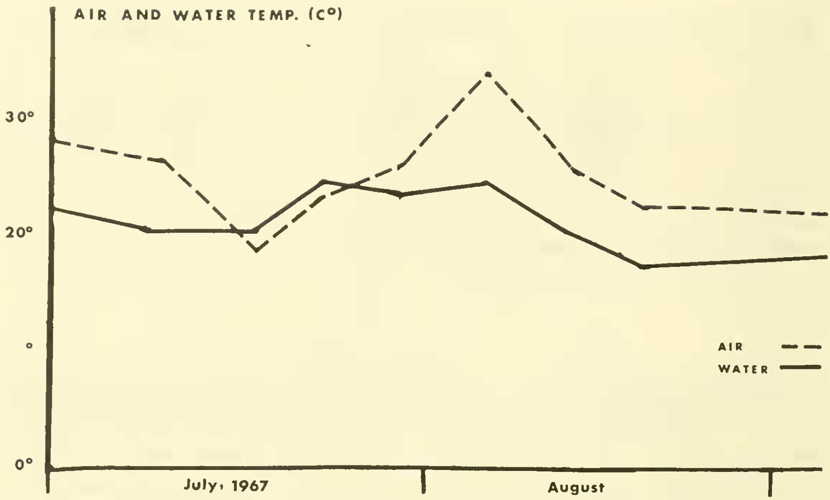

Fig. 4. Air and water temperatures recorded for July and August 1967. These represent daily recordings taken by Fisher at the lake.

mer seemed to occur immediately following a heavy rainstorm. Days in which rainfall exceeded one-fourth inch invariably resulted in adult salamanders being found in the swimming pool of the Brigham Young University Family Camp located two miles south of Salamander Lake. Adults were found in the pool at no other time.

We also noted that those larvae appearing on 30 July had an accelerated growth rate as compared to those hatched in June (Fig. 6). This we assume resulted because the water temperature was approximately 4 C warmer than in preceding weeks and remained warm for approximately two weeks after their appearance (Fig. 4). There was also a greater increase in vegetation and aquatic arthropods. Such factors are, we believe, the primary factors responsible for the rapid rate of development.

Apparently, heavy rain during the spring, summer, or fall months serves as a breeding stimulus to *Ambystoma tigrinum*. It is not unusual in Utah to find larvae of different ages in the mountain ponds and lakes. An entry in a field book (Tanner, 1938) indicates this size differential in several lakes on the SE rim of the Aquarius Plateau in late June. Such reproductive habits are seemingly appropriate for desert habitats where rains come irregularly. We note that tiger salamanders in Utah usually breed (lay eggs) at least once each year, usually in the spring.

In those individuals undergoing metamorphosis, it was observed that the general body appearance was changed and they appeared smaller—although total length was not substantially reduced. Upon removal of the stomach, it was noted, without exception, that the stomach was completely empty and appeared in a generally contracted condition. The stomachs of nonmetamorphosing individuals

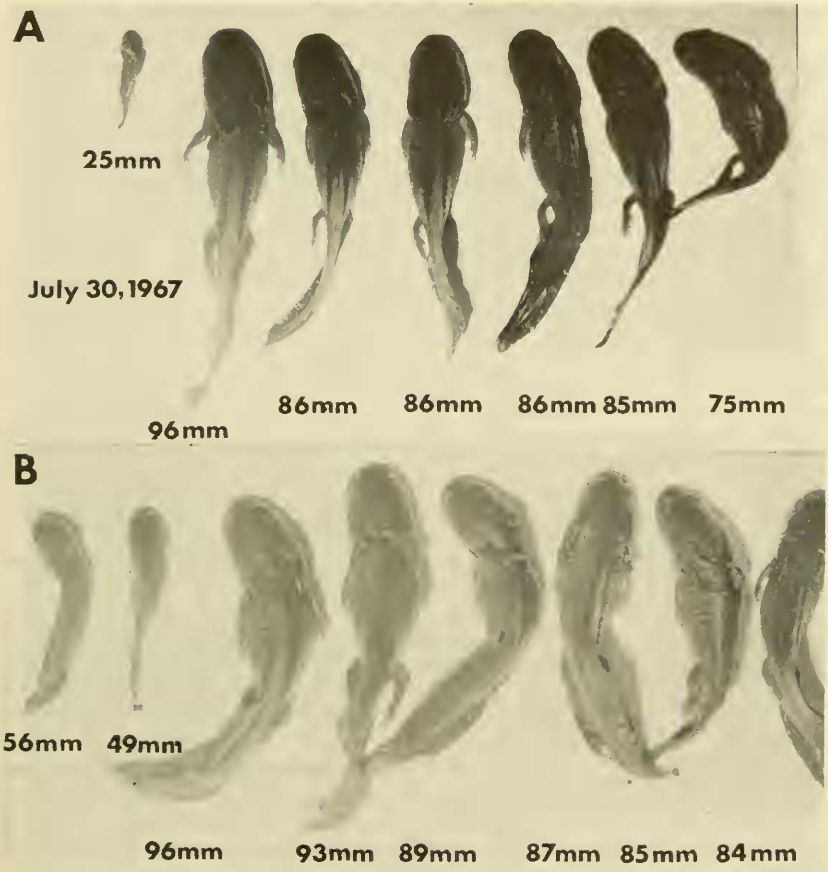

Fig. 5. Representative sizes of larvae as they appeared on (a), 30 July 1967, and (b), a second series as they appeared on 6 August 1967.

of the same collection contained food. It is evident that the larval forms do not feed, or do so sparingly, during the more active stages of metamorphosis. This is perhaps the result of the reabsorptions of the large dorsal and ventral fins of the tail and perhaps other organs.

We estimate, on the basis of our collecting data for 1967 (Fig. 6), that approximately 50 percent of the individuals were metamorphosed by the end of August. After a final exhaustive collection on October 11, only 3 larvae could be found in the entire lake. Under a log by the side of the lake, 1 small metamorphosed individual was also found. Most of the larvae seem, therefore, to complete metamorphosis by the end of one summer and to overwinter as young adults. Because weather conditions vary from year to year, we might expect considerable variation in the percentage of larvae that actually meta-

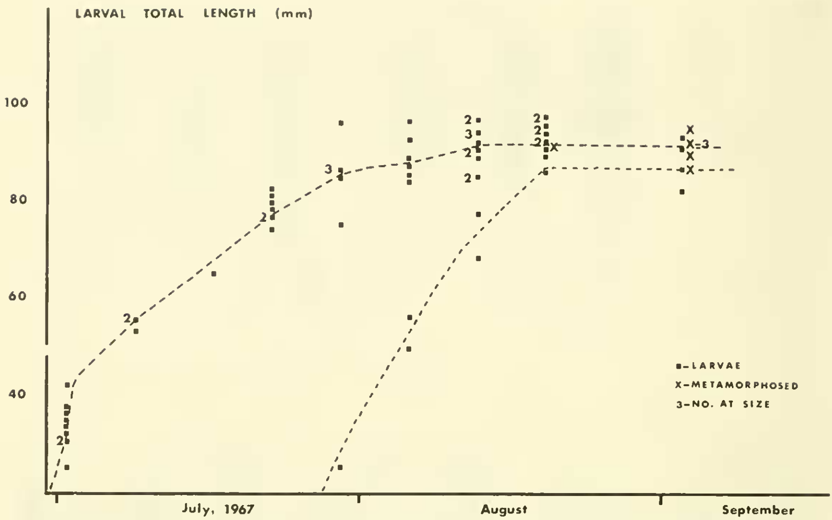

Fig. 6. Growth rates of the two age groups as they appear from July through August and into September.

morphose each year. In the spring of 1971, 5 large larvae were in the lake when it was first visited on 3 May. In 1970, large larvae were seen in the lake on 15 September, and, on 26 September, 10 larvae and 5 newly metamorphosed adults were found. The adults were only recently out of the small pond of murky water. They still had "gill buds" to indicate a recent transformation. The larvae were small and showed no signs of metamorphosis. There was only a small puddle of water remaining, an environmental hazard, which undoubtedly put stress on mature larvae to transform and results in the destruction of later generations whose morphological development is not complete. Only occasionally does this lake dry up, and it is obvious that late breeding occurring in August may result in young larvae unable to complete their growth before cold weather retards their development. Such larvae are carried over to the next spring if sufficient water is available; however, they do not occur in large numbers as compared with July of most years. Our observations indicate that heavy rains during the summer do trigger a breeding response on the part of a few adults after the main spring breeding season has passed. Such occasions provides two or more generations of larvae per year, some of which may not reach maturity until the next spring or summer.

Growth rate as indicated in figure 6 is dependent on several factors. Included among these are such items as: (1) An early or late spring permitting spawning at an early date. We note that snow and ice do not leave the lake at the same time each spring. In some cases there may be a time differential of three to four weeks. (2) Temperature variations resulting from cool, wet springs hold the temperatures down until later in the summer. Growth of larvae, as indicated, seems to be greatest during that part of the summer when water temperatures are greatest (25 C). In 1967 such a temperature occurred from mid-July to mid-August. However, this may also be modified if heavy rains persist during the months of July and August. (3) Salamander Lake is in a small basin and the accumulating water comes primarily from melting snow which had accumulated in drifts during the winter. If, therefore, large drifts are present, the cold runoff water retards the warming of the lake. (4) Weather conditions which would provide for an early development of aquatic growth would increase the food items available. We suspect that the abundance of food as well as favorable temperatures were responsible for the rapid growth of larvae hatched in July 1967.

We have not observed the extensive cannibalism in this population reported by Burger (1950) for a population in the Gothic area of Gunnison County, Colorado. We have not made extensive studies of food eaten, but have seen only a few instances of predation. Burger also projects a hypothesis that larvae require more than one growing season before metamorphosis occurs. It may be that the Gothic population at 8,000-10,000 ft would not have adequate time to mature, whereas the Salamander Lake population in Utah at about 7,000 ft does mature. We suspect, however, that what we have observed also occurs in Colorado—namely, that summer rains trigger late spring or summer breeding, which provides larvae of two sizes in the same pond. We also believe that overcrowding may result in cannibalism. We have not experienced a large larval population in any of the Utah ponds or lakes which has resulted in obvious cannibalism. In fact, during our extensive efforts in 1967, larvae were at times difficult to find in the heavy plant growth.

We have not found neotenic larvae thus far in any population of *A. tigrinum* in Utah. Axolotls do occur in *tigrinum* populations and one of us (Tanner) has either seen or collected such individuals from western Kansas and a pond near Shumway, Arizona. During the past 30 years, many populations have been observed throughout Utah without observing neoteny. We do not suspect that such a phenomenon cannot occur in the populations of the subspecies *nebulosum* but, rather, surmise that neoteny occurs where climatic and biotic factors do not place a heavy stress on the developing larvae. In desert or cold mountain habitats, periodic droughts limit the available aquatic habitats or destroy them. Cold weather, in which ice and snow reduce activity, limits or certainly circumscribes the activity of larvae. Such weather conditions reduce food production and may tend to reduce the cover normally found in a flourishing pond. Such stresses seemingly demand that larvae grow rapidly and metamorphose in order to escape from the rigorous and changing aquatic habitat. In contrast, a more uniform habitat such as those occurring in less variable climates are not placed under such stresses and can survive with equal success in the larval stage. We believe that such reasoning is plausible and may help to explain rapid larval growth and early metamorphosis in deserts and cold mountain habitats.

Literature Cited

Burger, W. L. 1950. Novel Aspects of the Life History of Two Ambystomas. Jour. Tenn. Acad. Sci. 25:252-257.

Hamilton, R. 1948. The egg-laying process in the tiger salamander. Copeia 1948:212-213.

Skousen, D. B. 1952. A taxonomic survey of the eggs and larvae of some species of Utah amphibia. Thesis of the Department of Zoology and Entomology, Brigham Young University, p. 10-12.

Tanner, V. M. 1931. A synoptical study of Utah amphibia. Proc. Utah Acad. Sci. 8:159-198.

Webb, R. G., and W. L. Roueche. Life History Aspects of the Tiger Salamander (*Ambystoma tigrinum*) in the Chihuahuan Desert. Gt. Basin Nat. 31:193-212.